

CRATAEGUS TENUIOR (ROSACEAE)—AN INTRIGUING NEW SPECIES FROM THE OKANAGAN OF BRITISH COLUMBIA AND WASHINGTON AND A NEW VARIETY OF *C. OKANAGANENSIS*

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ABSTRACT

The intriguing, red-fruited *Crataegus tenuior* has been known to the author for nearly 20 years and is finally described. The general appearance of *C. tenuior* is of a small, rather delicate *C. macracantha* but it differs in possessing \pm plane-sided nutlets, not a series *Macracanthae* character, conspicuously glandular leaf-teeth and variably glandular petioles, not normal characters of *C. macracantha*. From sympatric forms of the latter species it also differs in its bright pink anthers. Multivariate analysis used to clarify the distinction from sympatric *C. macracantha* also illuminates the regional variation of the latter species. A new variety of the purple-fruited *C. okanaganensis* (series *Purpureofractae*) is also described which has longer thorns, larger leaves, fewer stamens and much more copiously hairy inflorescences than the other varieties. *Crataegus okanaganensis* var. *longispina* is described and illustrated.

KEY WORDS: *Crataegus tenuior*, new species, series *Macracanthae*, Rosaceae, British Columbia, Okanagan-Shuswap, Washington; *Crataegus okanaganensis* var. *longispina*, var. nov.

RESUMEN

El sorprendente *Crataegus tenuior* de frutos rojos ha sido conocido por el autor durante cerca de 20 años y es descrito finalmente. El aspecto general de *C. tenuior* es el de un pequeño y bastante delicado *C. macracantha* pero se diferencia por tener núculas con laterales \pm planos, que no es un carácter de la serie *Macracanthae*, dientes de las hojas claramente glandulares y peciolo variablemente glandular, que no son caracteres normales de *C. macracantha*. También se diferencia de las formas simpátricas de esa especie por sus anteras rosa brillante. Se realizó un análisis multivariante para clarificar la distinción de los *C. macracantha* simpátricos que muestra la variación regional de esta última especie. También se describe una nueva variedad de frutos púrpura *C. okanaganensis* (serie *Purpureofractae*) que tiene espinas más largas, hojas más grandes, menos estambres e inflorescencias mucho más pelosas que las otras variedades. Se describe e ilustra *Crataegus okanaganensis* var. *longispina*.

INTRODUCTION

Review of my accumulated duplicate collection prior to its recent dispersal revealed unfinished business in the taxonomy of Pacific Northwest *Crataegus*. The *Crataegus* described for that region can be divided into red-fruited or purple- to black-fruited groups based on color of their fully ripe fruit and both are represented in this paper. This paper describes *Crataegus tenuior*, sp. nov. (red-fruited), and *C. okanaganensis* var. *longispina*, new var. (purple-fruited), ensuring that the very rich variation encountered by the author in the general area of the British Columbia Okanagan is fully accounted for, at least as far as distinctive and repeatedly occurring forms is concerned.

CRATAEGUS TENUIOR

The red-fruited *Crataegi* of the Pacific Northwest were revised by Phipps (1998) with the species native to the Okanagan being in two series, ser. *Rotundifoliae* and ser. *Macracanthae*. The former contains *Crataegus chrysocarpa* and *C. sheila-hippsiae* and was revised for the region by Phipps and O'Kennon (2004). It is distinguished by plane-sided nutlets and glandular petioles. Series *Macracanthae*, with laterally pitted nutlets and eglandular petioles, is here represented only by *C. macracantha*. *Crataegus chrysocarpa* and *C. macracantha* are very wide-ranging species occurring from the Okanagan to the Atlantic.

The new species, *C. tenuior*, is local and, at first glance, very similar to the slender form of *C. macracantha* Lodd. ex Loud. var. *occidentalis* (Britt.) Kruschke. *Crataegus macracantha* var. *occidentalis*, with white anthers,

is the most usual form of *C. macracantha* west of the Rockies and is the only variety of the species so far recorded from British Columbia. *Crataegus tenuior* was first collected by myself and R.J. O'Kennon of BRIT in September 1993 in the Shuswap area of British Columbia but, in spite of the similarities alluded to above, several differences from *C. macracantha* var. *occidentalis* soon became apparent. These included: often more rounded leaf apices, generally smaller and less coriaceous leaves, small pink anthers, generally more slender thorns, and more delicate plant habit (Figs. 10, 11, 12). Moreover, *C. tenuior*, like *C. chrysocarpa*, but unlike *C. macracantha*, has the sides of the nutlets \pm plane or, occasionally, only irregularly and shallowly pitted, as well as glandular, sometimes strongly so, petioles. In addition, *C. tenuior* shares with sympatric forms of both *C. macracantha* var. *occidentalis* and *C. chrysocarpa* Ashe var. *chrysocarpa*, the most common form of the latter species, the trait of ripening fruit passing through an apricot to salmon or orange phase on the way to ripening to a bright red (see *C. macracantha* - Figs. 13a, 12b), different from most other forms of both species, particularly those to the east of the Rockies, the fruit of which normally changes directly from green to red. However, in spite of sharing important characteristics with *C. chrysocarpa*, it is with a slender form of *C. macracantha* (Fig. 12b), sympatric with *C. tenuior*, that *C. tenuior* is most easily confused.

Crataegus tenuior proves to have a quite limited distribution predominantly in the northern Okanagan of southern British Columbia, mainly from somewhat north of Armstrong to the vicinity of Enderby in the north central Shuswap area where it is locally common. From this region it extends thinly into the generally drier Okanagan of Washington where *Crataegus* as a whole peters out. Mainly collected in the mid 1990s and 2002, *C. tenuior* remained undescribed until now because of the need to assess *C. macracantha* throughout its large range, the greatest of any North American *Crataegus*, prior to deciding whether it should be included in that species. Although *C. macracantha* has proven to be very variable through much of its range, especially so in Quebec and Montana, it has, except for a population in northwest Montana, strikingly eglandular petioles, a trait usually thought of as species-specific. Consequently, a morphometric study of relevant Pacific Northwest material was conducted to investigate these distinctions.

Morphometric study.—Fourteen flowering OTUs and 54 fruiting OTUs (Table 1), constituting all the former UWO (now TRT) specimens of putative *Crataegus tenuior* and *C. macracantha* from British Columbia and Washington, were used. The flowering specimens were scored for seven characteristics: mean length of three largest leaves, petiole glandularity (Figs. 9a, 9c), median thorn length, median thorn thickness, sepal margin serration (Figs. 9b, 9d), anther color (Fig. 11), and style number. The fruiting specimens used the same characters except that nutlet number replaced style number (it is usually the same) and nutlet lateral pitting replaced anther color. Missing data, if in less than 10% of OTUs, was replaced by column (character) means of the largest subset of OTUs considered, *a posteriori*, unequivocally the same taxon; if more than 10% missing that character would be rejected. Standard ordinations and cluster analyses were performed using Podani's SYN-TAX 2000. The data sets were ranged before analysis. The results are as follows:

i) Flowering material.

Cluster analyses of the euclidean distance matrix were by UPGMA (Fig. 1), complete link (CL, not shown), single link (SL, not shown) and incremental sum of squares, ISS (Fig. 2), thereby using some very contrasted methods. All show two major groups of seven OTUs each, these being *Crataegus tenuior* (OTUs 1–7, left) and *C. macracantha* (OTUs 8–14, right). UPGMA and CL are topologically identical. The SL result is topologically very similar to that for UPGMA while the very different-appearing ISS is topologically identical to UPGMA within *C. tenuior* but differs somewhat within *C. macracantha*.

The ordinations PoCA (Fig. 3) and MDS (Fig. 4) of the euclidean distance matrix similarly separate *Crataegus tenuior* and *C. macracantha* cleanly. The first axis of the principal co-ordinates analysis is responsible for 62% of the variation.

All six analyses of the flowering specimens sharply separate the same two groups, with one group always comprising seven specimens attributed to *Crataegus tenuior* and the other seven to *C. macracantha*. Although the sample size ($n=14$) is small, the concordance of very different methods emphasizes the robustness of the separation.

TABLE 1. Conciliation of OTU numbering in Figs. 1–8 with collection numbers. Collection numbers in parentheses. Collection numbers are all JBP numbers except 'Z' = P. Zika, 'WP' = Wm Phipps, and 'TCB' = TCBayshaw. For *Crataegus tenuior*, most of these specimens may be found among those cited, though not for *C. macracantha*.

Flowering specimens:	1 (6913), 2 (6918), 3 (6923), 4 (8370), 5 (8389), 6 (8400), 7 (8401), 8 (6902), 9 (6903), 10 (6963), 11 (8304), 12 (8306), 13 (8420), 14 (8421).
Fruiting specimens:	1 (6811), 2 (6814), 3 (6814a), 4 (7011), 5 (7013), 6 (7171), 7 (8265), 8 (8274), 9 (8451), 10 (8452), 11 (8453), 12 (8454), 13 (8470), 14 (8471), 15 (8472), 16 (8474), 17 (6782), 18 (6792), 19 (8275), 20 (8473), 21 (6484), 22 (7103), 23 (7025), 24 (6783), 25 (8457), 26 (6778), 27 (6802), 28 (WP1.5), 29 (8456), 30 (6794), 31 (6790), 32 (6781), 33 (6787), 34 (6793), 35 (8176), 36 (6782), 37 (8275a), 38 (6976), 39 (6786), 40 (6779), 41 (8477), 42 (TCB4041), 43 (8463), 44 (8464), 45 (8478), 46 (6789), 47 (6867), 48 (6871), 49 (Z17891), 50 (Z17907), 51 (Z20320), 52 (17904), 53 (Z22423), 54 (7265).

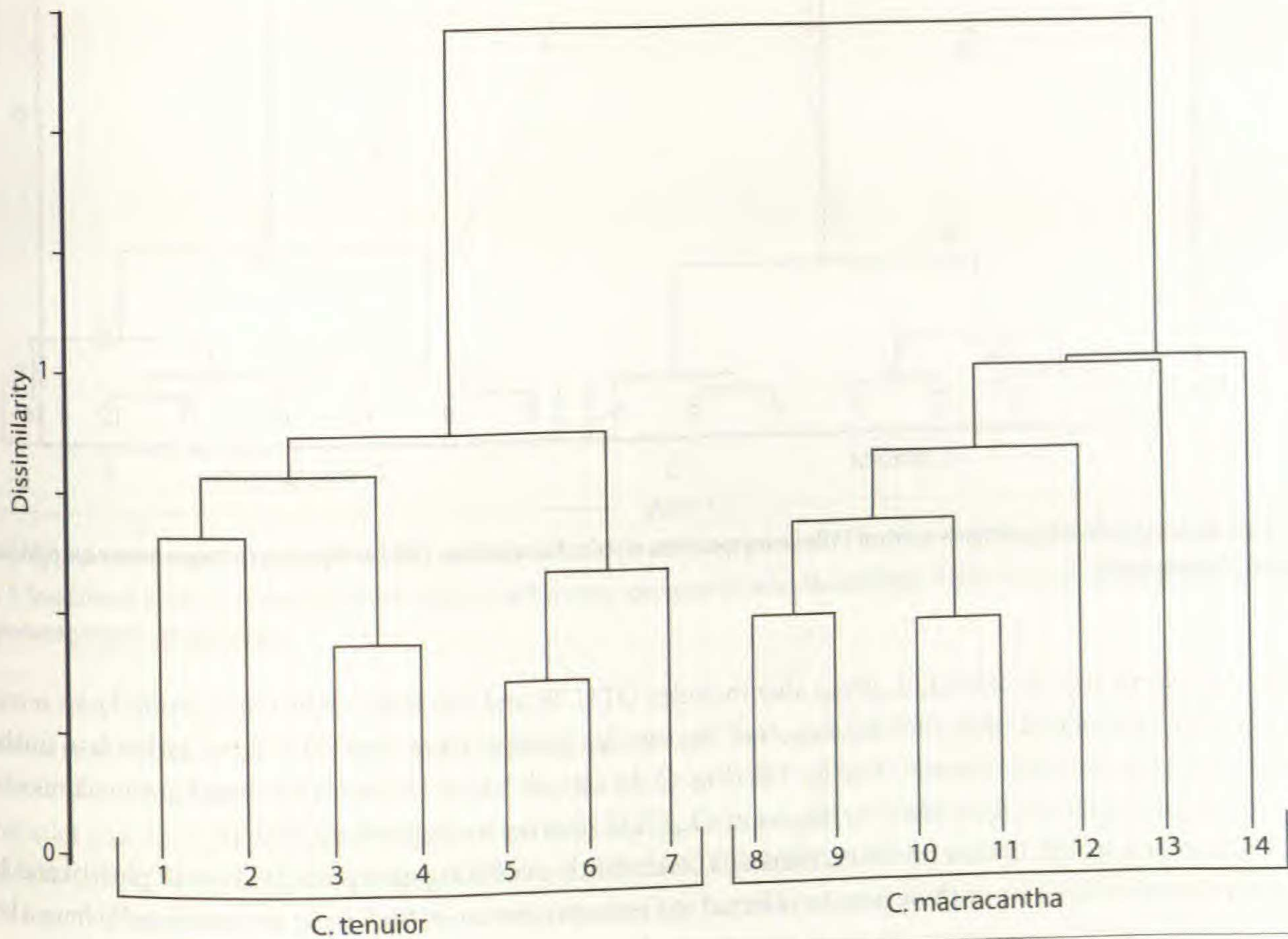


FIG. 1. UPGMA clustering of euclidean distance matrix of 14 flowering specimens of series *Macracanthae*. Left-hand group is *Crataegus tenuior* and right-hand group is *C. macracantha*.

The *Crataegus tenuior* OTUs all had pink anthers, \pm entire to denticulate sepal margins, 3 or 4 styles, short thorns (mean = 40.14 mm) and short leaves (mean = 41.66 mm) while *C. macracantha* var. *occidentalis* OTUs had white or ivory anthers, more deeply serrate sepal margins, 2 or 3 styles, short to longer (mean = 51.4 mm) thorns and short to longer leaves (mean = 47.00 mm).

ii) **Fruiting material.**

The same four methods of cluster analysis were applied to the much larger sample of fruiting data (n=54). UPGMA (Fig. 5) finds a left-hand cluster of OTUs 1–16 plus 19 and 26, to which is added the very isolated 54, and a much larger right-hand group. There is also an extreme isolani (OTU 22) in Figure 5 which is the most isolated OTU of all and adds on after fusion of the two larger groups. CL, not shown, identifies the same left-hand cluster of OTUs 1–16 plus 19 and 26, with the remaining OTUs clustering in two fairly large groups with several specimens apparently even more isolated than OTUs 22 and 54. SL, also not shown, is very similar to the

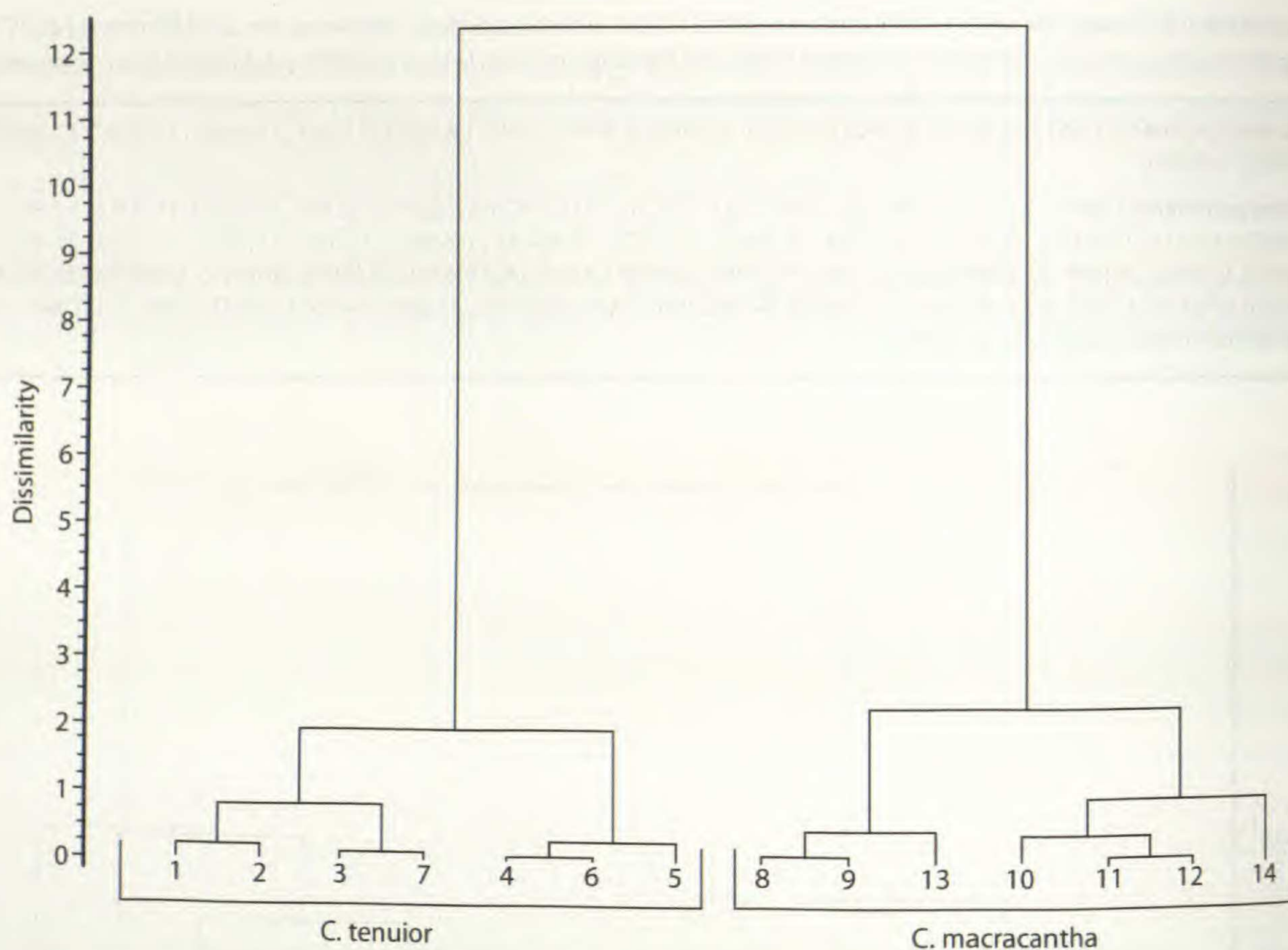


FIG. 2. ISS clustering of euclidean distance matrix of 14 flowering specimens of series *Macracanthae*. Left-hand group is *Crataegus tenuior* and right-hand group is *C. macracantha*.

UPGMA except that its left-hand group also includes OTU 39 and the large right-hand group lacks several OTUs which are added only after the fusion of the two big groups. Here also OTU 22 is added last, further emphasizing its isolated position. Finally, ISS (Fig. 6) divides all 54 OTUs into a left-hand group identical to that in UPGMA and the remainder. In this, as in CL, OTU 22 is not as isolated as OTU 54.

Summarizing the cluster analyses, there is a consistently occurring group of OTUs 1–16 plus 19 and 26. At least the great majority of these may be referred to *Crataegus tenuior* as they lack, or occasionally have a low level of nutlet pitting or scarring. Similarly, the remainder, comprising a large right-hand group, outliers, if any, to the left-hand group of *C. tenuior*, plus outliers, if any, to the combined main groups, may in large part be referred to *C. macracantha* as they have higher scores for nutlet pitting. OTUs 22 and 54 are notable outliers in the dendrograms.

Among the ordinations, PCoA (Fig. 7) yields a left-hand group of OTUs 1–16 plus 19 and 22 and a large group of the remainder. Here 41% of total variation is picked up by the first axis. MDS (Fig. 8) yields a top-right group of OTUs 1–16 plus 19 with OTU 22 by itself at top left and a bottom-left group of the remainder. In this OTUs 26 and 54 are peripheral. This strong isolation of OTU 22 in MDS reflects the UPGMA situation. As with the cluster analyses, a discrete *Crataegus tenuior* group may be found that is characterized by a lack of, or at most, a low level of, nutlet pitting or scarring. And as in the flowering analyses, all the OTUs with four nutlets lie in the putative *tenuior* group except for the isolated OTUs 22 and 54. Significantly, the two very different ordination methods identify the same main patterns of variation and also detect very similar groups to those of the cluster analyses with some inconsistencies regarding OTUs 22 and 26. The fruiting analyses are thus somewhat less mutually similar than the flowering analyses, an observation in line with the lower percentage of variance accounted for by axis 1 of the PCoA.

In all the fruiting analyses *Crataegus tenuior* occurs as a similar core grouping of OTUs 1–16 + 19. In these

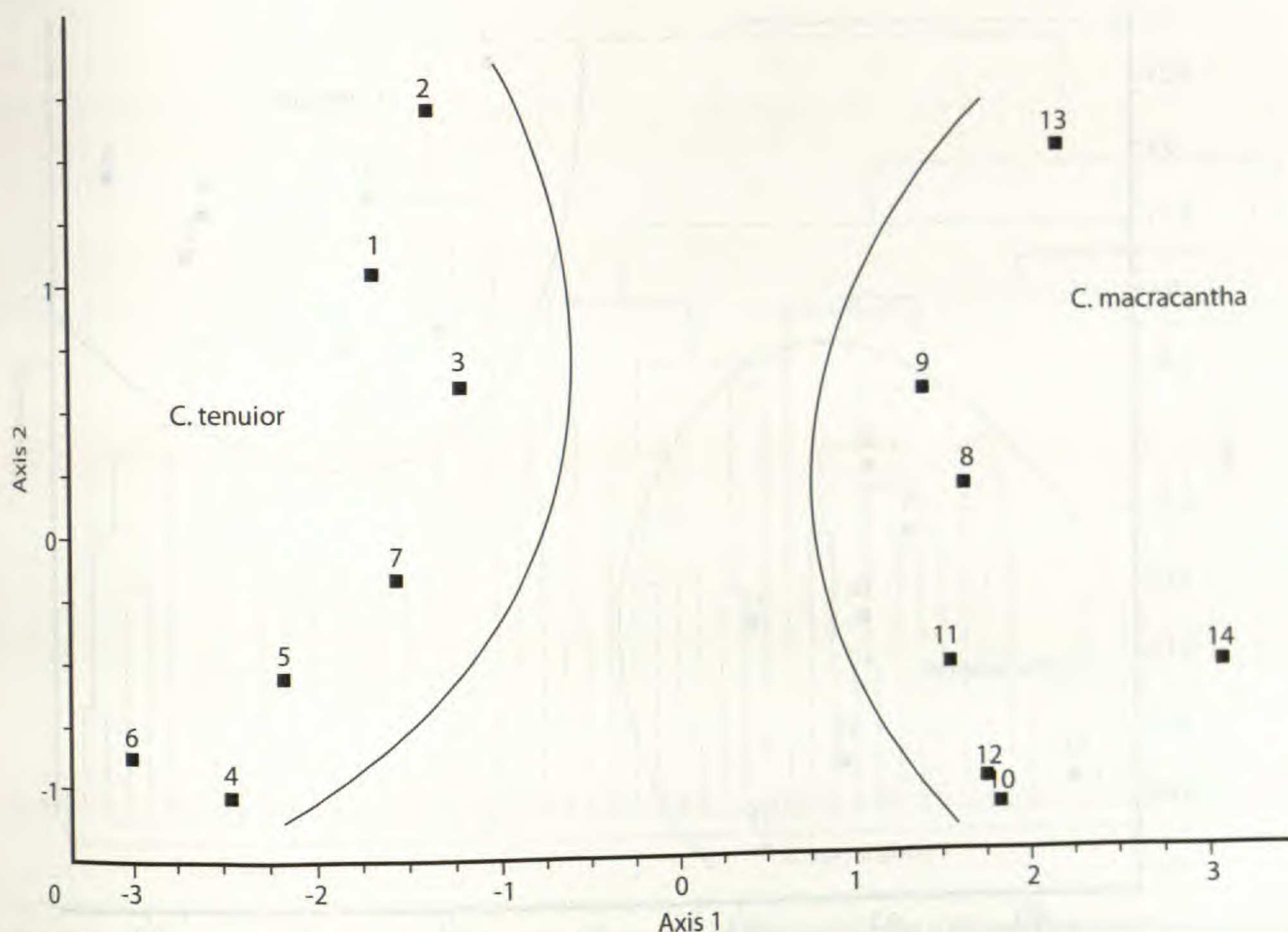


FIG. 3. Standardized PCoA of euclidean distance matrix of 14 flowering specimens of series *Macracanthae*. Left-hand group is *Crataegus tenuior* and right-hand group is *C. macracantha*.

analyses, the core *tenuior* group contains those specimens with plane-sided or nearly plane-sided nutlets (scores of 0–1 on a three-point scale), glandular petioles, subentire to barely serrate sepal margins where this character could still be reliably interpreted in fruit, and short thorns. In UPGMA (Fig. 5) the core *tenuior* group splits into three subgroups containing: OTUs 4, 5, 7, 9, 13; OTUs 1, 2, 3, 6, 8, 11, 12, 14, 15; and OTUs 10, 16, 19, the first and last of which have higher petiole glandularity than the second subgroup though the significance of this is not clear. Similar subgroups are found in Figure 6 (ISS) and they may also be detected in the ordinations (Figs. 7, 8). It is, of course, a feature of glands that they may be subject to abrasion through the season so what may be a more constant character at anthesis can be less well-defined later. OTU 19 is the only specimen grouping with the *tenuior* core that has a middling nutlet score (1.75) so is not entirely typical.

Crataegus macracantha is represented by all of the remaining OTUs (17–18, 20–54) in the fruiting analyses except OTU 22, see below, interpretation. All the OTUs in the 17–18, 20–54 *macracantha* group, plus OTU 22, have nutlet sides significantly (score of 2) to strongly (score of 3) pitted, except for OTUs 26, 27 and 54 which have middling nutlet side scores (respectively 1.25, 1.75, 1.5). OTUs 26 and 39 are 'floaters' that may sometimes cluster loosely with the core *tenuior* group though both ordinations place them in the *macracantha* group but in the part closest to the *tenuior* group. Within the *macracantha* group UPGMA (Fig. 5) has a left-hand cluster containing OTUs 17, 18, 20, 21, 29, 30, 32, 34, 36, 48, 42, 53 that mainly comprises the smaller-leaved specimens with dimensions more like *C. tenuior*. The non-*tenuior* OTUs are arranged rather differently in the various analyses, a fact particularly seen in both the inconsistent positioning of more isolated OTUs and in the CL dendrogram that is not shown. A major reason for this is presumably that the fruiting sample is much larger than the flowering one (54 OTUs compared to 14), and therefore more diverse, this no doubt due to the much longer time-frame over which adequate specimens can be collected.

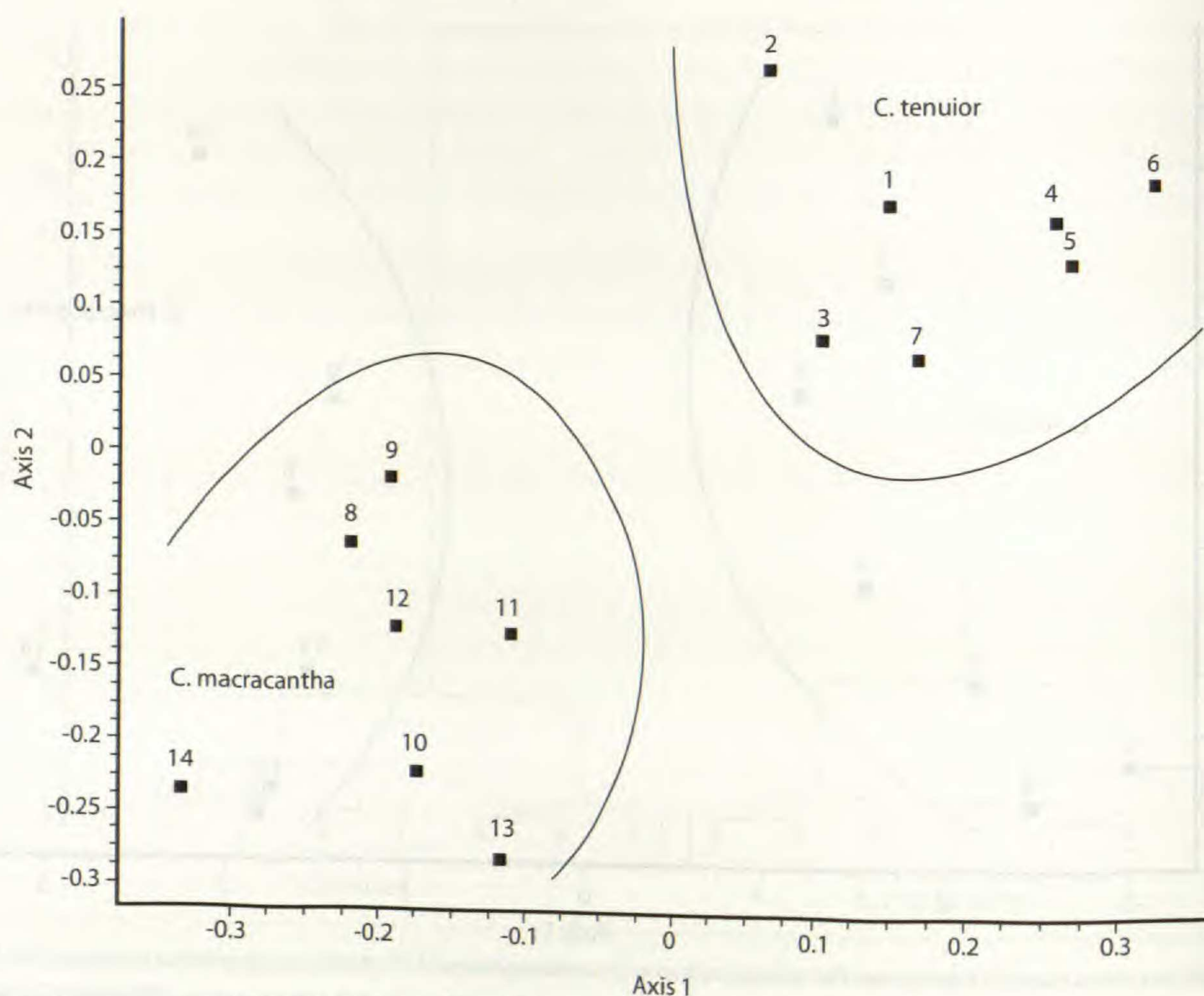


FIG. 4. Plot of MDS of euclidean distance matrix of 14 flowering specimens of series *Macracanthae*. Top-right group is *Crataegus tenuior* and bottom-left group is *C. macracantha*.

iii). Interpretation.

The flowering OTUs separate cleanly into two groups with clear character differences as mentioned above. However, in the more numerous fruiting OTUs more variation is present and two mutually exclusive groups do not emerge. Nevertheless, a group of 1–16 + 19 is consistently found which is *Crataegus tenuior*. In fruit, the best interpretation seems to be to accept the presence of plane-sided nutlets as decisive for this species and to consider petiole glandularity a more variable character that scores low to high in *tenuior* compared to nil (usually) or low in putative *macracantha*. As well, a few OTUs, e.g., fruiting 26, may be atypically intermediate or perhaps hybrid between the two main groups.

Whereas a *Crataegus tenuior* group may be readily recognized in the fruiting results, the non-*tenuior* OTUs display several problems with their lower level of cohesion. On the one hand, they suggest that there may be fundamental differences between large and small-leaved *macracantha*. However, the study was not set up to test this and, minimally, would have required a greater range of leaf characters to do so. Also, OTU 54 is an oddity, perhaps cultivated, from the post office at Mara, northern Okanagan. This is clearly a *C. macracantha* form with its eglandular petioles and pitted nutlets but it possesses a leaf shape differing from all other *macracantha* individuals in the study, as well as very villose parts, again quite unlike the others studied. Some of its more distinct features did not get measured in this study which has a different objective and furthermore, being thornless, it achieved thorns of mean length as is necessary for missing data in SYNTAX. Thus, OTU 54 is in actuality more distinct than the analyses show and perhaps represents a human import to its locality. It has resemblances to *C. macracantha* var. *pertomentosa* (Ashe) Kruschke. Quite different, however, from the main mass of *macracantha* is fruiting OTU 22 from Tonasket, Washington (Fig. 14). This individual appears the most

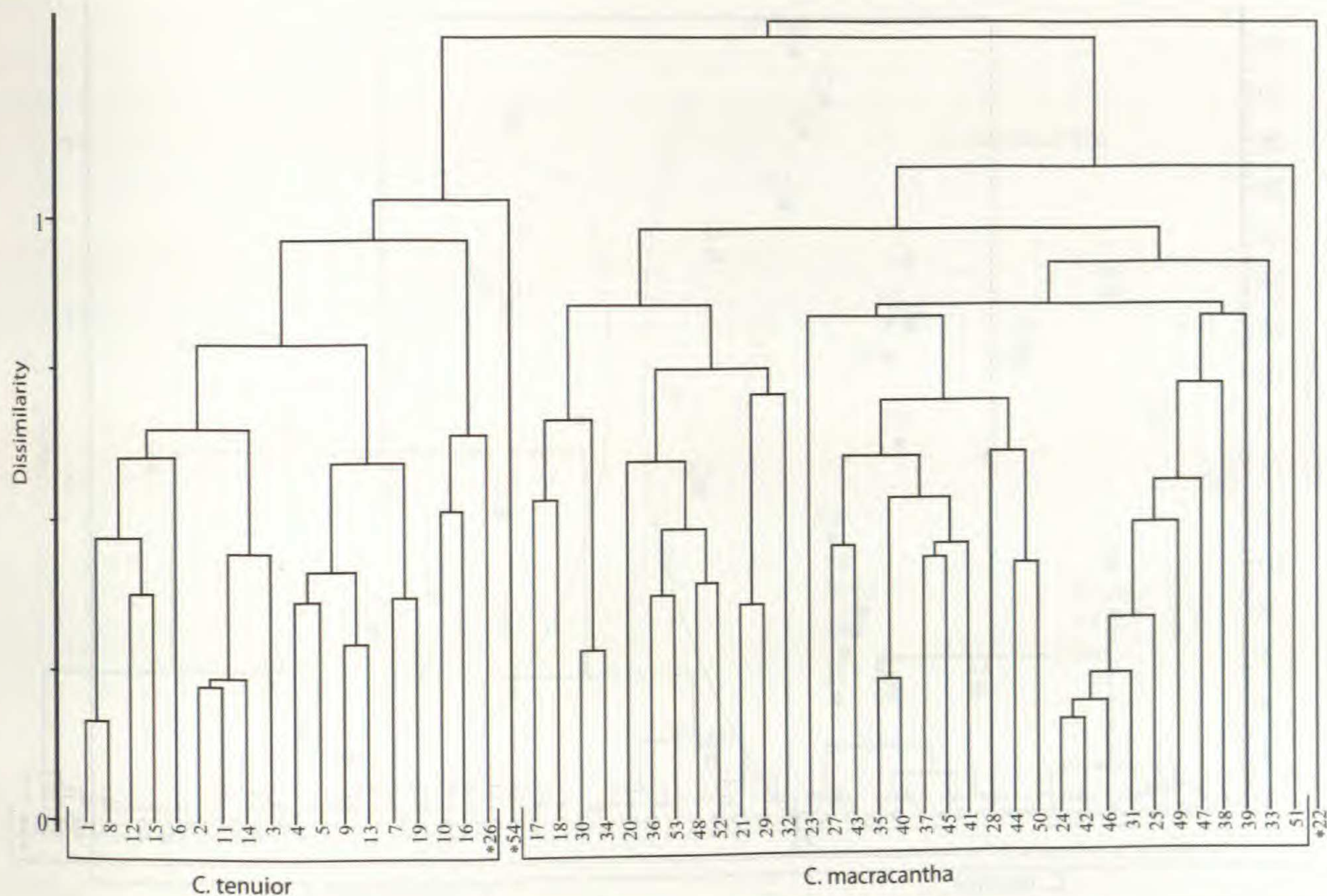


FIG. 5. UPGMA clustering of euclidean distance matrix of 54 fruiting specimens of series *Macracanthae*. Core of left-hand group is *Crataegus tenuior* and right-hand group is *C. macracantha*. OTUs 22, 26 and 54 are starred. Note isolation of OTU 22.

extreme of all in UPGMA and MDS, is second most extreme in ISS and is peripheral in PcoA. It is the only OTU in the study to combine four nutlets, highly glandular petioles, and deeply pitted nutlet sides. Unlike *C. tenuior*, it has essentially glandless leaf-teeth at $\times 10$. Also, it is the only specimen of the 68 studied to have a distinctively non-macracanthoid leaf shape, one with clear resemblances to *C. chrysocarpa*. This, I suspect, is a very rare example in the study area, perhaps unique in collections, of an F_1 hybrid or clone thereof, between *C. chrysocarpa* and *C. macracantha* var. *occidentalis*.

Confirmation that the calibration of fruiting and flowering groups to taxonomic names is consistent is shown by two flowering specimens attributed to *Crataegus tenuior* (JBP 6814 and JBP 8401) being from the same plants as JBP 7171 and JBP 8454 (fruiting) while for *C. macracantha* var. *occidentalis* JBP 6903 (flowering) comes from the same plant as JBP 6871 (fruiting).

Crataegus tenuior J.B. Phipps, sp. nov. (Figs. 9–11). TYPE: CANADA: BRITISH COLUMBIA: Okanagan, Shuswap valley, just E of Enderby, JBP Phipps 6913, 5 May 1994 (HOLOTYPE: TRT; ISOTYPES: DAO, UBC, V, WTU).

Frutices, 2.5–4.0 m alti, multicaules; ramuli unius anni \pm castanei vel rubrobrunnei, veteres cinereo-brunnei; spinae 3–5 cm longae, rectae vel leviter recurvatae, \pm tenues, in juventute nitenter atrospadiceae. Folia decidua: petioli 1.25–2.5 mm longi, pubescentes solum in sulco, aliquando glandulomaculati; laminae (2.5–)3–5(–7) cm longae, late-ellipticae vel ovatae vel rhombovatae, apicibus subacutis, basibus \pm late-cuneatis, vadositer 4–5(–6) lobatis per latus, lobis acutis vel obtusis, marginibus serratis, serris conspicue nigro-glandulosis (\pm integribus in parte tertia basali excepta), venatione craspedodroma, venis 5(–6) per latus, adaxialiter inconspicue impressis in maturitate, superficiebus adaxialibus dense et breviter appressis-villosis, superficiebus abaxialibus glabris, leviter pubescentibus per venas, textura tenui et colore autumnali luteo. Inflorescentiae ca. 10-floratae, ramulis tomentosis, bracteolis caducis, linearibus, membranaceis, glandulo-marginatis, glandibus subsessilibus. Flores 15–17 mm diam.; hypanthium extrinsecus dense pubescens; sepala anguste triangularia, marginibus \pm glandulo-denticulatis, abaxialiter \pm glabra; petala \pm circularia, alba; stamina 5–10, antheris roseis, saepe parvis (ca. 0.6 mm); styli 3–4. Fructus ca. 8–10 mm diam., \pm late ellipsoidales, in juventute aurantiaci, in maturitate clare coccinei, varie villosi, reliquis sepalorum \pm appresso-patentibus; pyrenae 3(–4), dorsaliter sulcatae, lateribus \pm planis vel irregulariter et vadositer erosis.

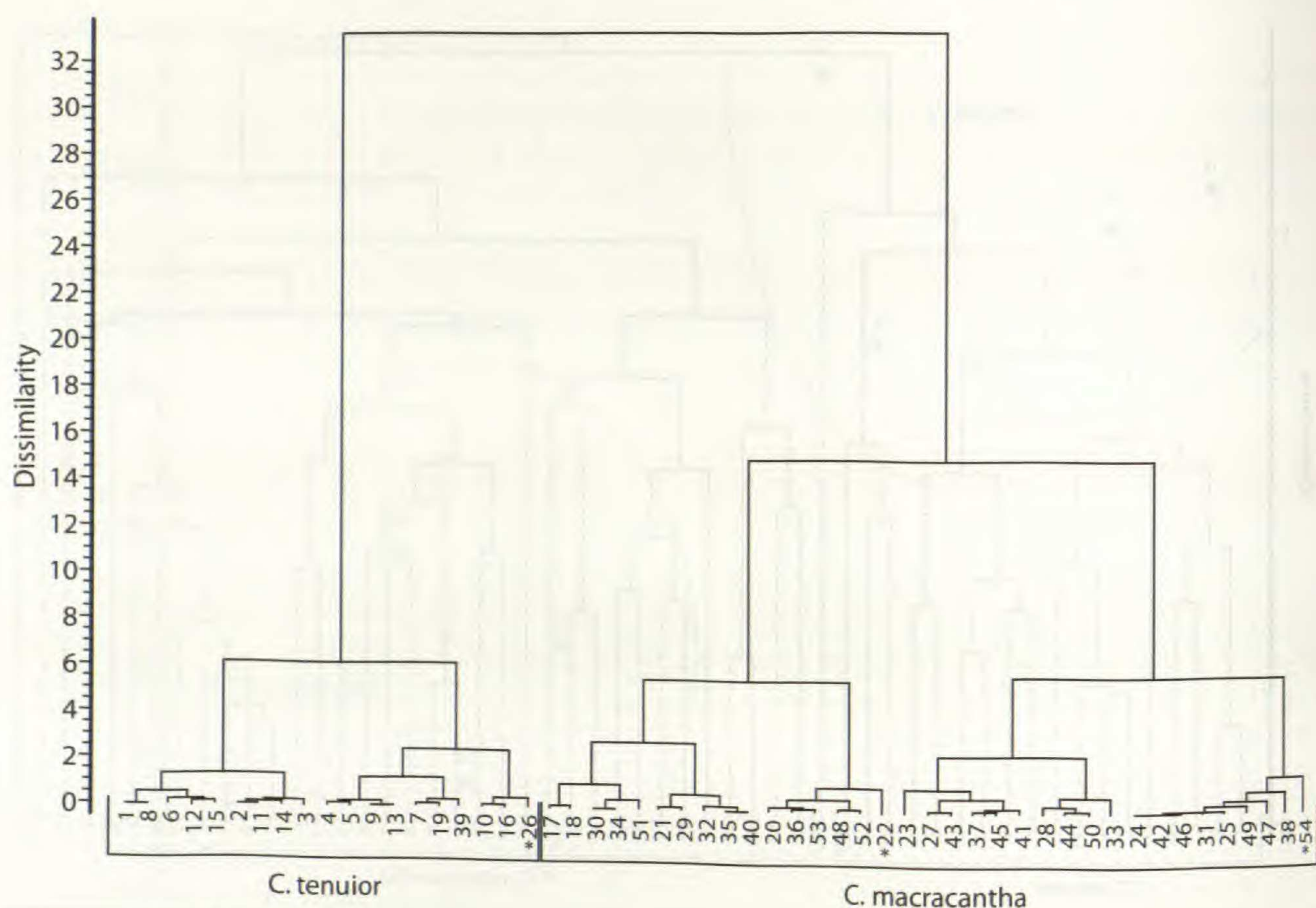


FIG. 6. ISS clustering of euclidean distance matrix of 54 fruiting specimens of series *Macracanthae*. Core of left-hand group is *Crataegus tenuior* and right-hand group is *C. macracantha* + OTU 22. OTUs 22, 26 and 54 are starred.

Bushes, 2.5–4.0 m tall, multi-stemmed: 1-year old twigs tan to reddish brown, older gray-brown; thorns 3–5 cm long, straight to slightly recurved, thinnish, glossy black-chestnut when young. Leaves deciduous; petioles 1.25–2.5 cm long, pubescent only in sulcus, variably gland-dotted; blades (2.5–)3–5(–7) cm long, broadly elliptic to ovate or rhombovate in general shape; apices subacute, bases broad-cuneate, shallowly 4–5(–6) lobed per side, lobes acute to obtuse; margins serrate, teeth with conspicuous black marginal glands (except \pm entire in basal third), venation craspedodromous with 5(–6) pairs of lateral veins, veins adaxially not strikingly impressed at maturity, adaxially densely short-appressed hairy, abaxially thinly pubescent on the veins, otherwise glabrous, texture thin, autumnal color bright yellow. Inflorescences abt. 10-flowered; branches tomentose, bearing caducous, linear, membranous, gland-margined bracteoles, glands subsessile. Flowers 15–17 mm diam.; hypanthium externally densely pubescent; sepals narrow-triangular, margins \pm glandular-denticulate, abaxially \pm glabrous; petals \pm circular, white; stamens 5–10, anthers pink, often small (ca. 0.6 mm); styles 3–4(–5). Fruit ca. 8–10 mm diam., \pm broad-ellipsoid, orange when young, brilliant red at maturity, variably villous; calyx remnants present, \pm appressed-spreading; nutlets 3(–4), dorsally furrowed, their faces \pm plane or irregularly and shallowly eroded.

Crataegus tenuior is most easily distinguished in flower (Figs. 9, 11) when it differs from sympatric *C. macracantha* by a variety of characters as discussed above. In fruit, however, *C. tenuior* may be difficult to distinguish from smaller-leaved specimens of *C. macracantha* without dissection of the pomes. This is because the petiolar glandularity character has some overlap, the sepal margin character may be difficult to discern, the plane-sided nutlets, though shown by the numerical analyses to be definitive for the species, are not evident without dissection, and the nutlet number of three, most frequently found, is not diagnostic. At that stage, therefore, one may use for macroscopic identification specimens tagged at flowering time although autumnal leaf color (yellowish in *C. tenuior* vs. bronze in sympatric *C. macracantha*) makes for a helpful distinction, as

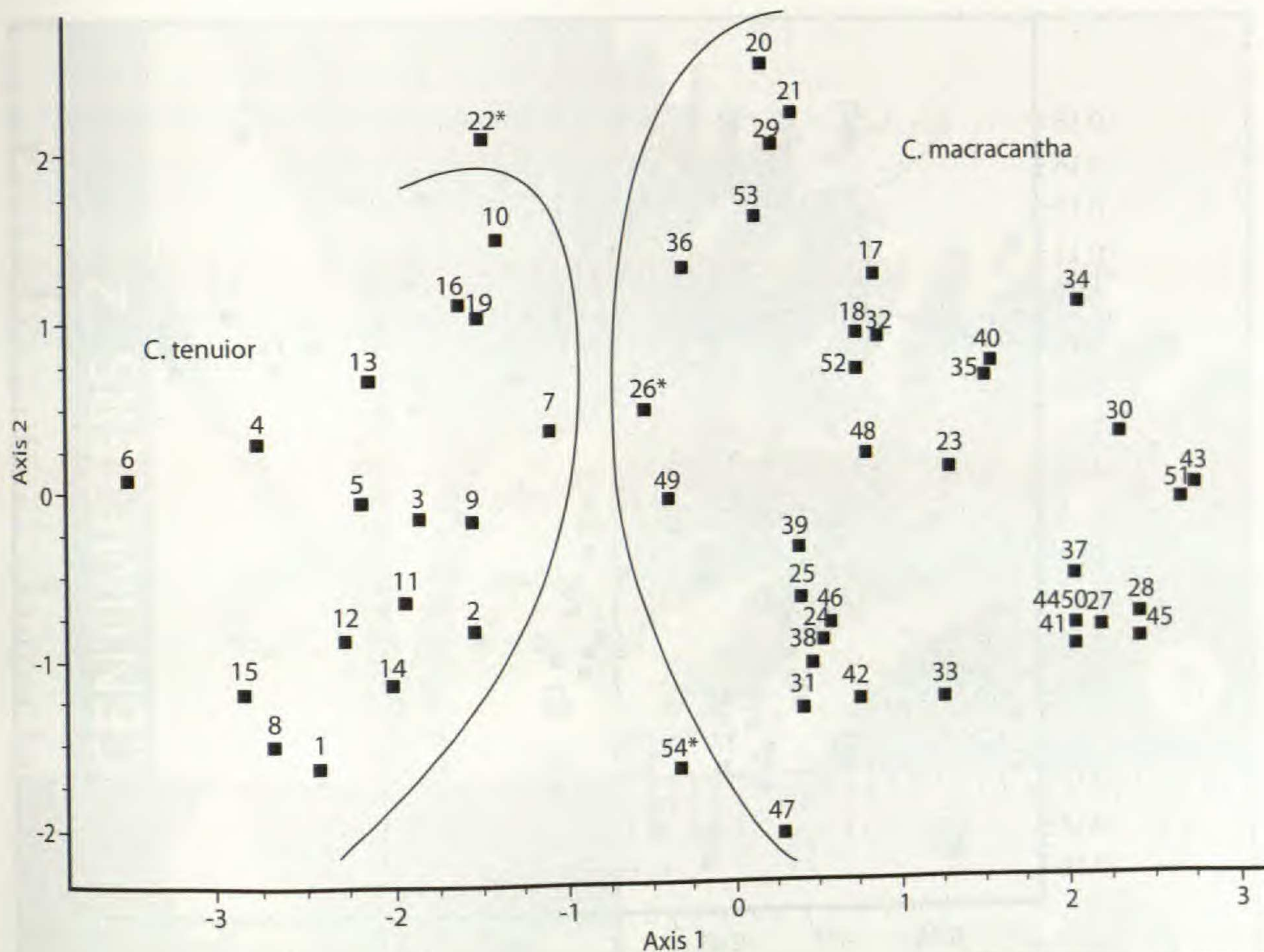


Fig. 7. Standardized PCoA of euclidean distance matrix of 54 fruiting specimens of series *Macracanthae*. Left-hand group is *Crataegus tenuior*; right-hand group is *C. macracantha*; OTUs 22, 54 excluded. OTUs 22, 26 and 54 are starred.

may the smaller leaves, and greater delicacy of habit, twig, thorn, and leaf texture with the more robust forms of *C. macracantha*. With regard to *C. chrysocarpa*, in spite of sharing several characters in common with *C. tenuior*, see key, it has such a different facies that it is easily separated macroscopically. The following key summarizes critical distinctions between *C. tenuior*, *C. macracantha* var. *occidentalis* and sympatric *C. chrysocarpa* var. *chrysocarpa* in the context of all the red-fruited *Crataegi* of the Okanagan. Note that with fruiting material it is best to check several fruits for nutlet pitting.

KEY TO RED-FRUITED CRATAEGUS SYMPATRIC WITH *C. TENUIOR*

- 1. Leaves deeply lobed, sometimes nearly to midrib; veins to sinuses; stamens 20, anthers pink-purple; styles and nutlets 1 ***C. monogyna***
- 1. Leaves shallowly lobed; veins to sinuses lacking; stamens usually 10, anthers cream or pink; styles and nutlets 2–4(–5).
- 2. Autumnal leaf color usually bronze; petioles eglandular; stamens 10, anthers cream; sides of nutlets strongly pitted ***C. macracantha* var. *occidentalis***
- 2. Autumnal leaf color usually yellow; petioles more or less glandular; stamens 10 or 20, anthers ivory (cream) to pink; sides of nutlets smooth. ***C. sheila-hippsiae***
- 3. Stamens 20, anthers pale pink ***C. tenuior***
- 3. Stamens 10, anthers pink or ivory (cream).
- 4. Plant habit lax; twigs in second year reddish-brown or deep reddish-brown; leaf-teeth with conspicuous (to a ×10 lens) glands; anthers pink; styles and nutlets 3(–4) ***C. chrysocarpa* var. *chrysocarpa***
- 4. Plant habit stiff; twigs in second year ± fawn or grayish-fawn; leaf-teeth with very small (just visible with a ×10 lens) or no glands; anthers ivory; styles and nutlets 3–4(–5)

Additional differences between *Crataegus tenuior* and *C. chrysocarpa* var. *chrysocarpa* exist in the form of the leaves. In fact, the two are normally distinguishable on this character alone with experience even though it is difficult to express this in words. Also, the latter taxon, being the most xeromorphic western *Crataegus*, can be

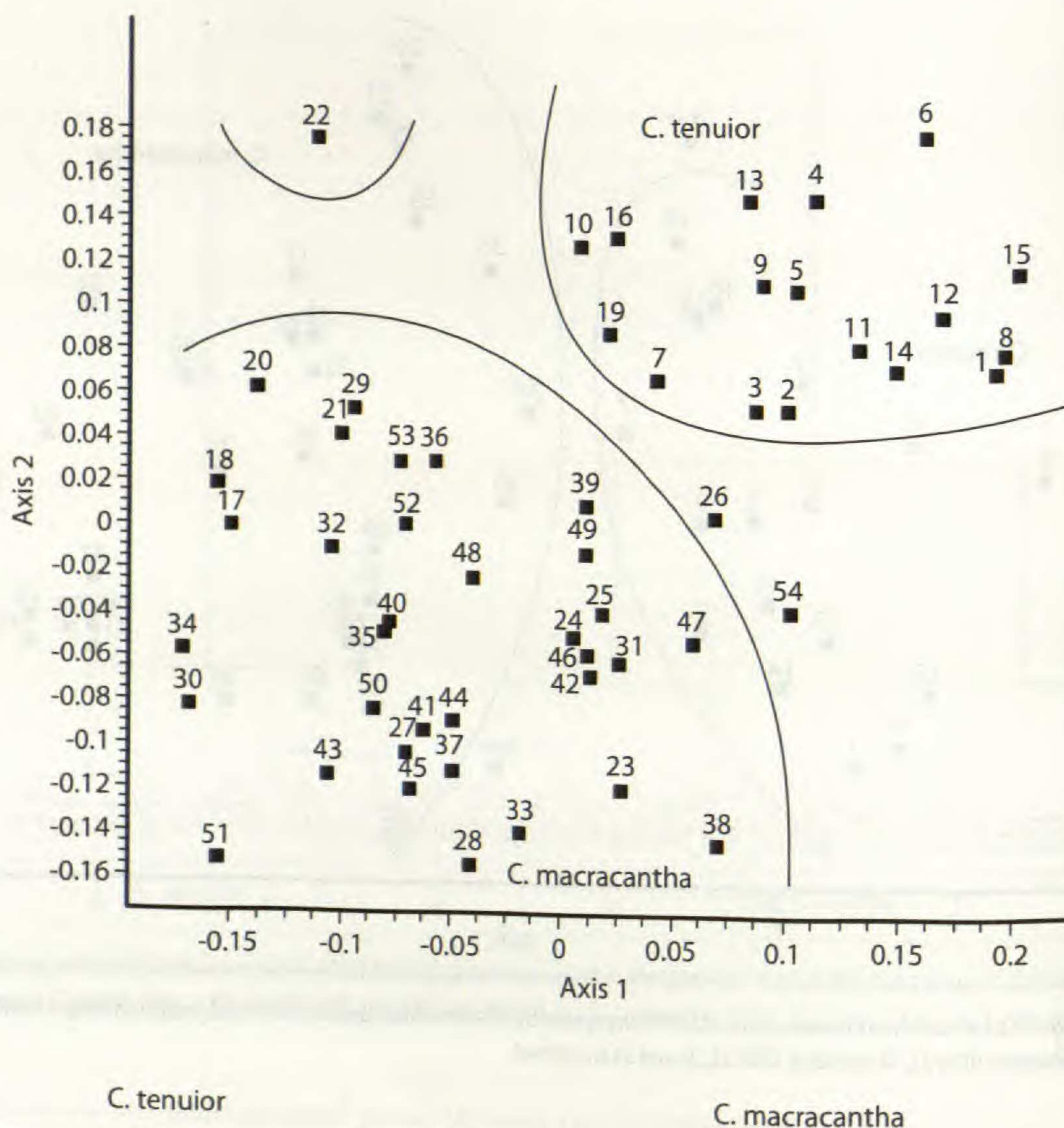


FIG. 8. Plot of MDS of euclidean distance matrix of 54 fruiting specimens of series *Macracanthae*. Upper right group is *Crataegus tenuior* and lower left group is *C. macracantha*. Note isolation of OTU 22.

found in drier habitats than *C. tenuior* even though there is much overlap. With regard to *C. macracantha* var. *occidentalis*, much more floriferous inflorescences and larger leaves may be found in many (Figs. 12, 13) than in *C. tenuior* (Figs. 9, 10), though again there is considerable overlap in these traits due to the frequent occurrence of smaller-leaved and smaller inflorescence forms of *C. macracantha*.

Relationships and possible origins.—*Crataegus tenuior* is a local species with obvious similarities to, and equally strong differences from, the very widespread *C. macracantha* so it is tempting to consider it of hybrid origin with that species. Further, being a red-fruited hawthorn whose fruit passes through the typical orange phase of most western *Crataegus* and possessing the plane-sided nutlets and glandular petioles of the equally common and also sympatric *C. chrysocarpa*, the latter is another candidate parent especially as there are so few red-fruited native *Crataegi* in the area. However, *C. tenuior* possesses conspicuous (with a $\times 10$ lens) gland-tipped leaf-teeth, as well as pink anthers, unlike either of *C. macracantha* or *C. chrysocarpa* from British Columbia or Washington. However, in spite of differing anthesis times, *C. macracantha* \times *C. chrysocarpa* is the suggested origin for the sporadic *C. laurentiana* (Quebec, etc.), as well as a similar but more abundant, unnamed form in Minnesota, and perhaps the variable and recently resurrected *C. sheridana*, widespread in the Great Plains (Phipps & O'Kennon 2007). Still, it is notable that, in spite of the abundance and sympatry of *C. macracantha* and *C. chrysocarpa* in the greater Okanagan, apparent first or early generation hybrids are hardly ever seen, let alone collected (except perhaps OTU 22, this paper). This being so, the distinctive Okanagan en-

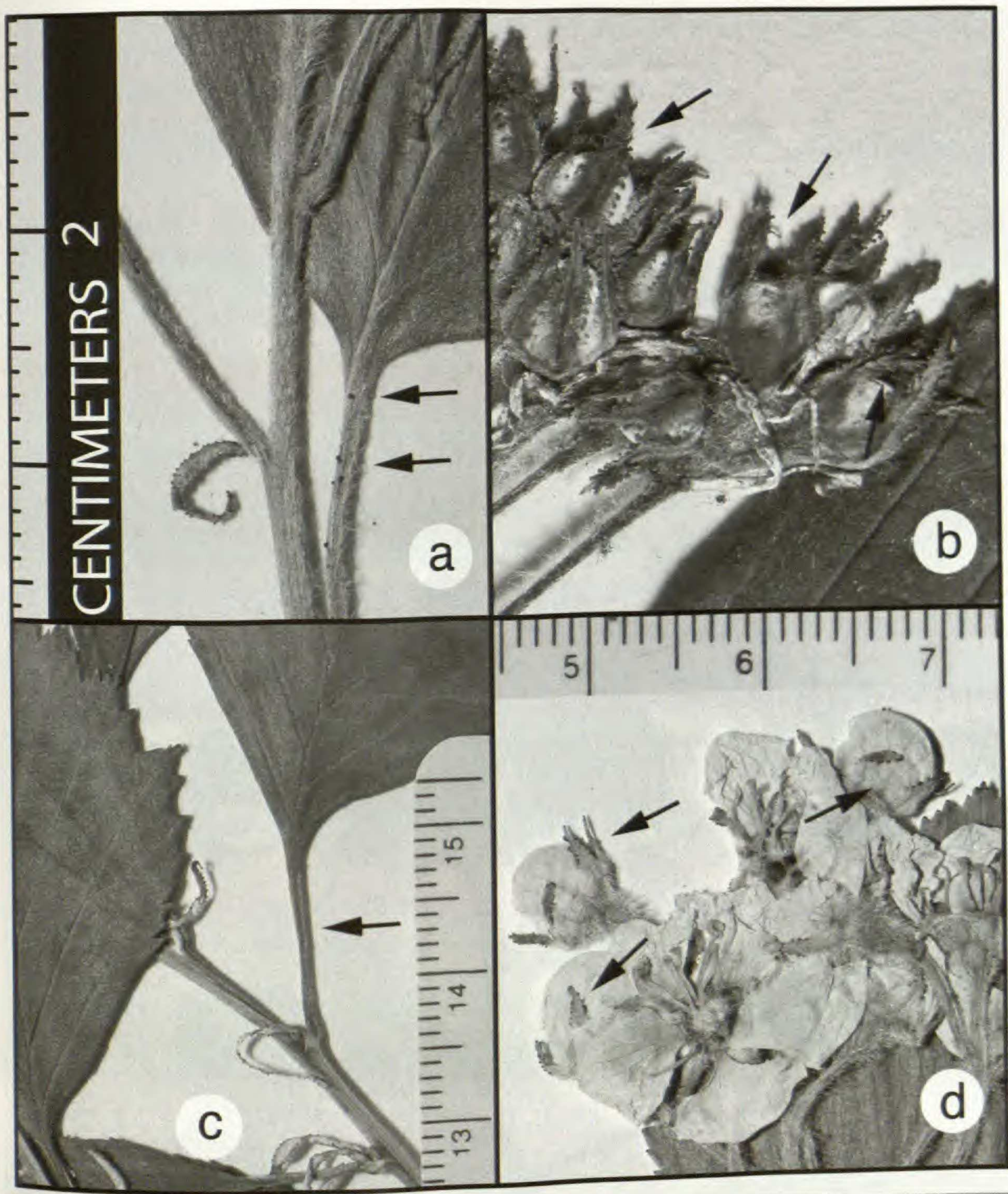


FIG. 9. Comparisons of petioles and inflorescences of *Crataegus tenuior* (Phipps 6913, holotype) and *C. macracantha* var. *occidentalis* (Phipps 6902); a) eglandular petioles of *C. macracantha*; b) deeply serrate sepal margins in *C. macracantha*; c) glandular petioles of *C. tenuior*; d) denticulate sepal margins in *C. tenuior*.

demic *C. atrovirens* (ser. *Purpureofractae*), which has pink anthers and the larger type of leaf marginal gland, could instead be considered a candidate parent. But *C. tenuior* shows no suggestion of the plump, ampulliform, purple, large-sepal fruit of *C. atrovirens*. Also, the latter species is recorded as having pitted nutlets. Thus, in lack of precise intermediacy between any two sympatric taxa, adaptive radiation cannot be discounted as a mechanism of origin and resolution of the matter must await molecular study. In passing, one may speculate that the small-leaved form of *C. macracantha*, noted at the beginning and in discussion of the morphometric results, might represent introgression or hybrid origin between *C. tenuior* and the larger-leaved *C. macracantha* var. *occidentalis*.



FIG. 10. Part of holotype of *Crataegus tenuior* (Phipps 6913, nr. Enderby, British Columbia).

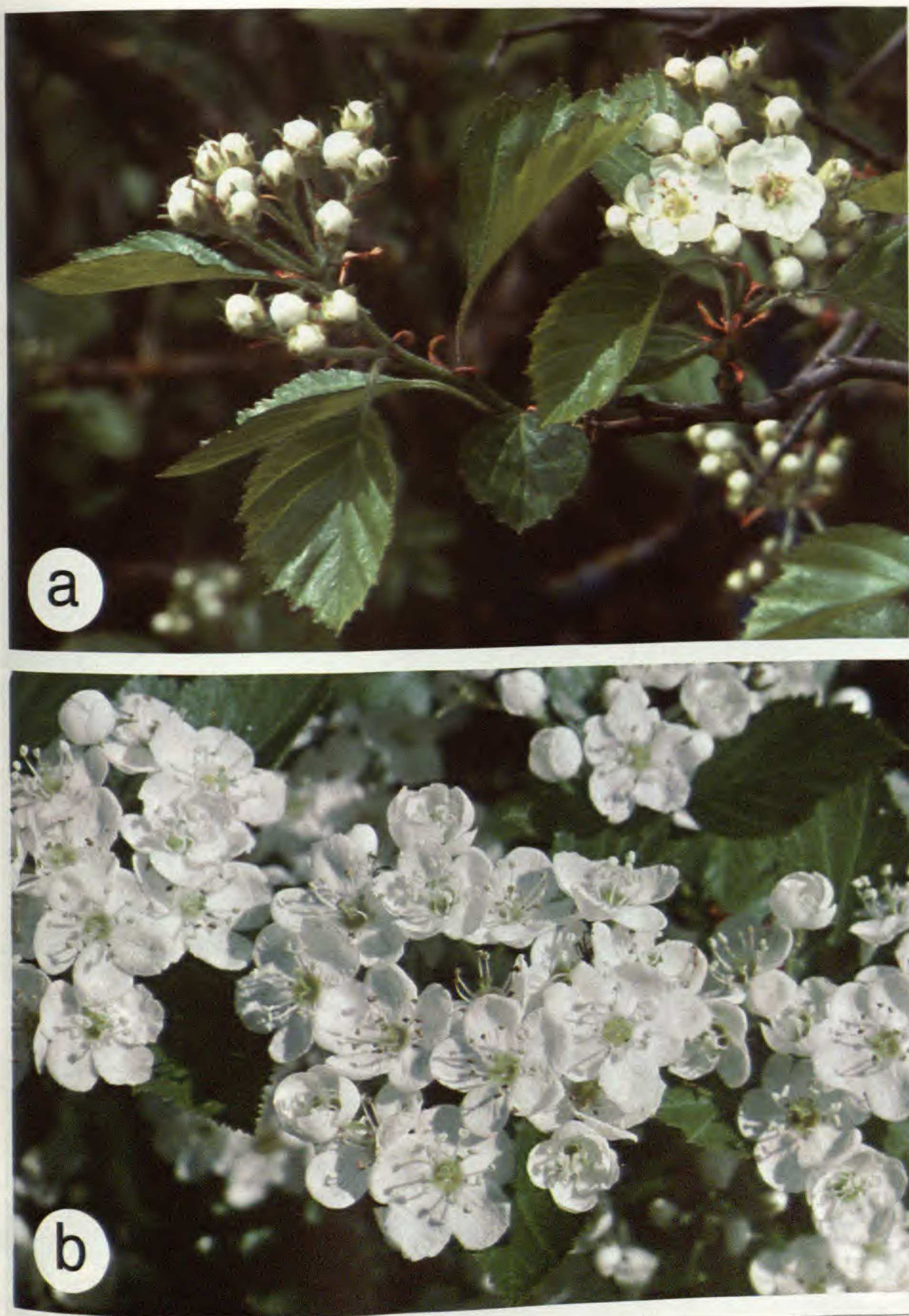


FIG. 11. Photographs of flowering specimens: **a)** *Crataegus tenuior* (Phipps & O'Kennon 8370); note pink anthers; **b)** *C. macracantha* (Phipps 6963); note cream anthers, larger inflorescence.

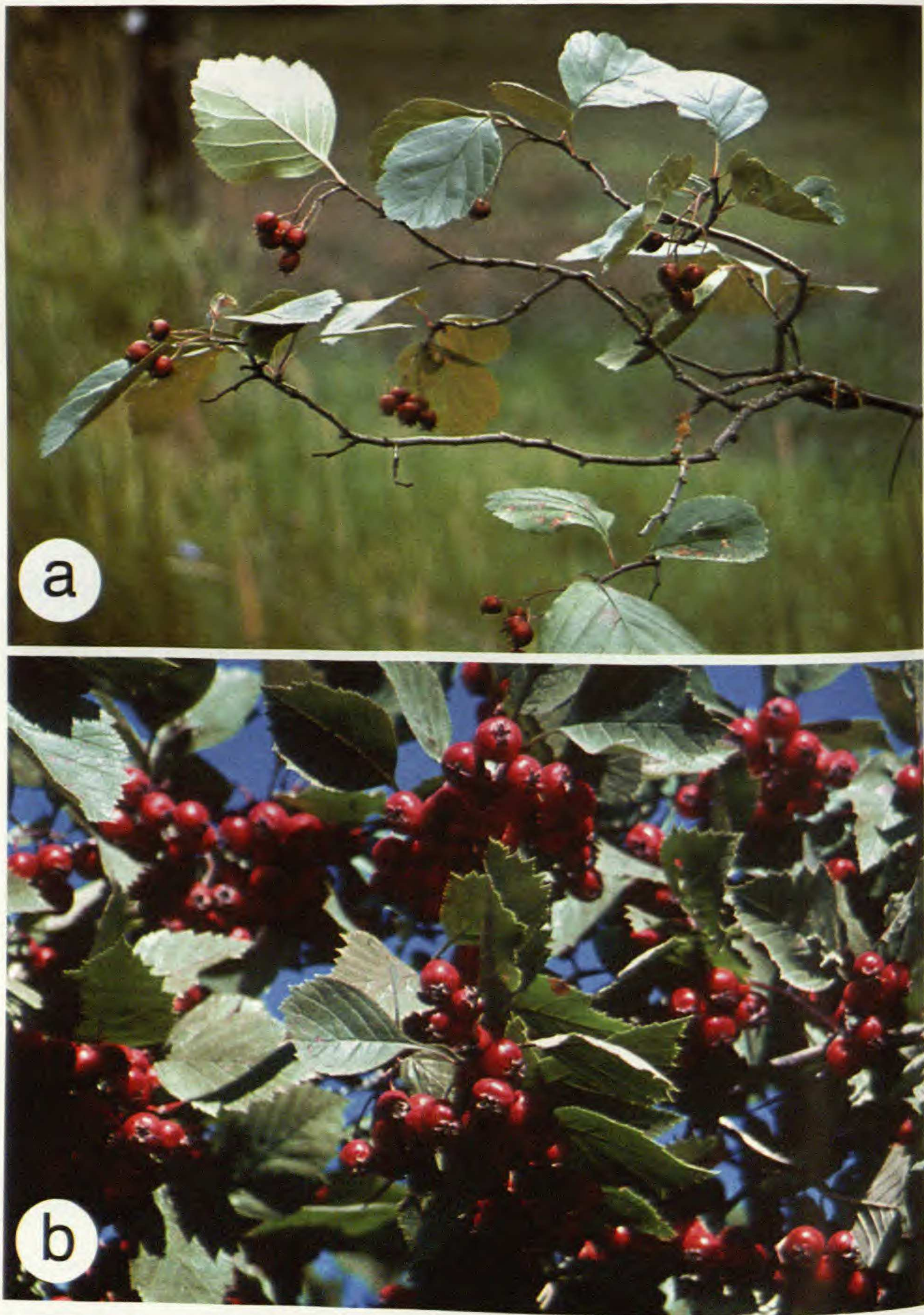


FIG. 12. Contrast of fruiting specimens of: a) *Crataegus tenuior* (not collected, Inch Logan Rd, nr. Enderby, BC); b) *C. macracantha* var. *occidentalis* showing deep red mature fruiting stage (not collected, Palmer Lake, WA; photo R.J. O'Kennon). Note differences in leaf shape, stiffness and coriacity, delicacy/robustness of twigs, number of fruit in infructescences.

Other macracanthoid western hawthorns with some similarities to *Crataegus tenuior*.—It is worth drawing attention to the following additional western populations with some *Crataegus tenuior* characteristics. In the Mogollon Mts. of New Mexico a small and isolated population of a macracanthoid *Crataegus* with glandular petioles is known. This is represented by O'Kennon, Huff & Snowden 13427 (TRT, flowering), Huff *et al.* 1380 (UNM 86261, fruiting), and Kirkeminde 897 (UNM 83115, fruiting) and has the further features of pink-purple anthers and yellow autumnal color but clearly pitted nutlets. This population lies well to the south of the southernmost populations of *C. chrysocarpa* in central Colorado but too little is known it about to warrant further comment. Rather similar populations of *C. macracantha* in Arizona have pink-purple anthers and pitted nutlets though typically eglandular petioles—such populations appear scarce west of the Rocky Mountain front, the region dominated by var. *occidentalis* and there is an unconfirmed report by Nadia Talent (pers. comm.) from Gregory Canyon, Colorado. Also, in northwest Montana there is a substantial population of a pink-anthered, glandular-petioled, pitted-nutlet morphotype closely resembling *C. macracantha*.

CRATAEGUS OKANAGANENSIS VAR. LONGISPINA

Crataegus okanaganensis (ser. *Purpureofructae*) is a large hawthorn with stout thorns, readily distinguished from *C. douglasii* and immediate allies not only by thorn measurements and fruit color but by the serial characteristic of typically large, pointed, fruiting sepals in contrast to the much smaller, often blunt ones found in ser. *Douglasianae*. The following key distinguishes the *Purpureofructae* of the Okanagan.

1. Leaf blades of a broader form, elliptic to broad-elliptic or suborbiculate or broad-ovate to ovate-elliptic; lobes short, tips obtuse to subacute; fruit oblong or subspherical.
2. Leaf blades elliptic to broad-elliptic or suborbiculate, lobes acute, strikingly pale green at anthesis; inflorescences only thinly hairy; sepals narrow-triangular; pomes 7–10 mm diam., ± oblong, claret in late August, becoming deep burgundy in September ***Crataegus orbicularis***
2. Leaf blades broad-ovate to ovate-elliptic, lobes subacute to obtuse, mid green at anthesis; inflorescences densely pubescent; sepals broad-triangular; pomes ± 12 mm diam., subglobose, bright or deep red in August, becoming nearly black in September ***Crataegus phippsii***
1. Leaf blades narrow-ovate to rhombic-elliptic or elliptic else ovate to rhombovate, lobes ± sharp; fruit ampulliform or rarely subspherical.
3. Thorns usually ± stout, 2–4 cm; leaf-blades rhombovate, ovate or elliptic-oblong, ± glossy, shiny mid to deep green, ± coriaceous; stamens 5–10, anthers nearly always cream or white; sepals in fruit erectopatent to reflexed, narrow; pomes bright to deeper red late August, becoming dark purple in September.
4. Leaf blades 3.5–6 cm, coriaceous, without strongly impressed venation adaxially, flattish to strongly concave, usually mid-green until fall ***Crataegus okanaganensis***
4. Leaf blades 4–8 cm, softly coriaceous, with distinctly impressed venation adaxially, flattish to convex, usually deep green until fall ***Crataegus enderbyensis***
3. Thorns usually ± slender, 3–5(–7) cm; leaf-blades elliptic to broad-elliptic or narrow-ovate to rhombovate, matte, deep dull green; not coriaceous; stamens 10 or 20, anthers pink; sepals in fruit suberect, broad, herbaceous; pomes deep burgundy in late August, purple-black in September ***Crataegus atrovirens***

Crataegus okanaganensis var. *longispina* (Figs. 15–17) is represented by a series of specimens that in most technical characters resemble the typical, common, variety of the species but differ in their much longer thorns, often much larger leaves, much more densely pubescent, even tomentose, inflorescence branches and hypanthia, 5–6 normally pale pink anthers, and usually more hairy fruit. This ensemble of characteristics is not found in the common varieties of *C. okanaganensis*, a fruiting specimen of which is illustrated in Figure 18 for comparison, and for this reason a new variety is recognized.

Crataegus okanaganensis var. *longispina* is a local taxon found in British Columbia in the southeastern Shuswap region, from Enderby to Salmon Arm.

***Crataegus okanaganensis* J.B. Phipps & O'Kennon var. *longispina* J.B. Phipps, var. nov. (Figs. 13–17).** TYPE: CANADA: BRITISH COLUMBIA: SW Shuswap region, N of Enderby, Anderson Rd., bush 7 m tall, fruit plum-red, 5 filament bases, 7 Sep 2001, JB Phipps & RJ O'Kennon 8281 (HOLOTYPE: TRT; ISOTYPE: UBC).

Frutices, 3–8 m alti; ramuli novelli dense pubescentes, eis unius anni mid- vel atro- nitentes rubro-brunnei; spinae 4–7 cm longae, atro-rubro brunneae vel atrae, ± tenues, rectae vel leviter recurvatae. Folia decidua, petiolata; petioli ca. 25–30% longi quam laminae, ± pubescentes, dense sic in sulcis, eglandulares vel cum sparsis glandis nigris parvis; laminae rhomb-ovatae (vulgo) vel late ellipticae, 4.5–9(–10) cm longae, saepe ± convexae, basibus ± late-cuneatis, (2–)3–4 lobatae per latus, max. IFI ca. 15% (in laminis angustioribus) - 25% (in laminis

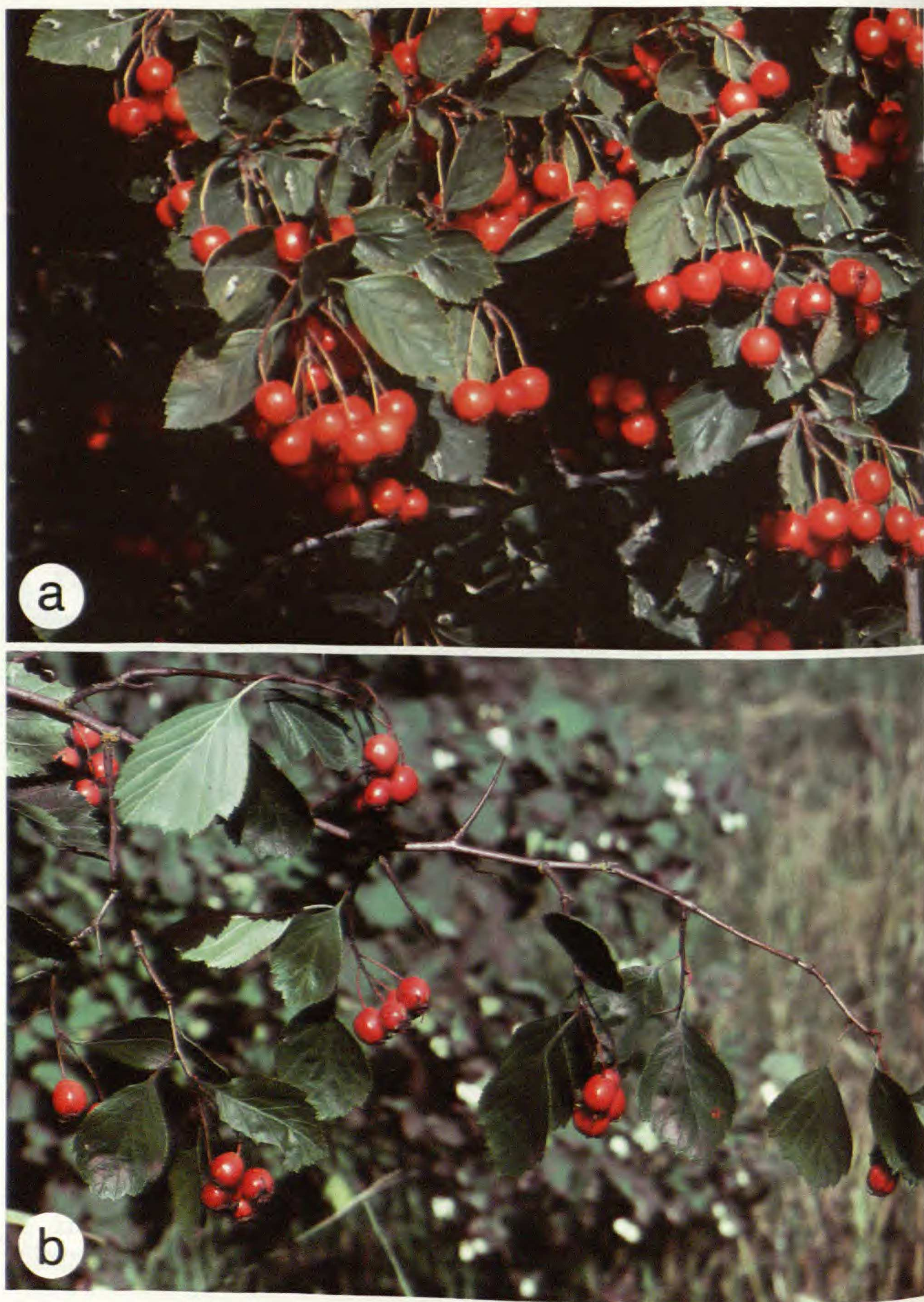


FIG. 13. Comparison of fruiting specimens of *Crataegus macracantha* var. *occidentalis*. a) stouter form showing typical orange-colored earlier fruiting stage (not collected, Palmer Lake, WA; photo R.J. O'Kennon); b) more delicate form (Phipps 6814, Shuswap valley, BC). Note differences in leaf shape, stiffness and coriacity, delicacy/robustness of twigs, number of fruit per infructescence.

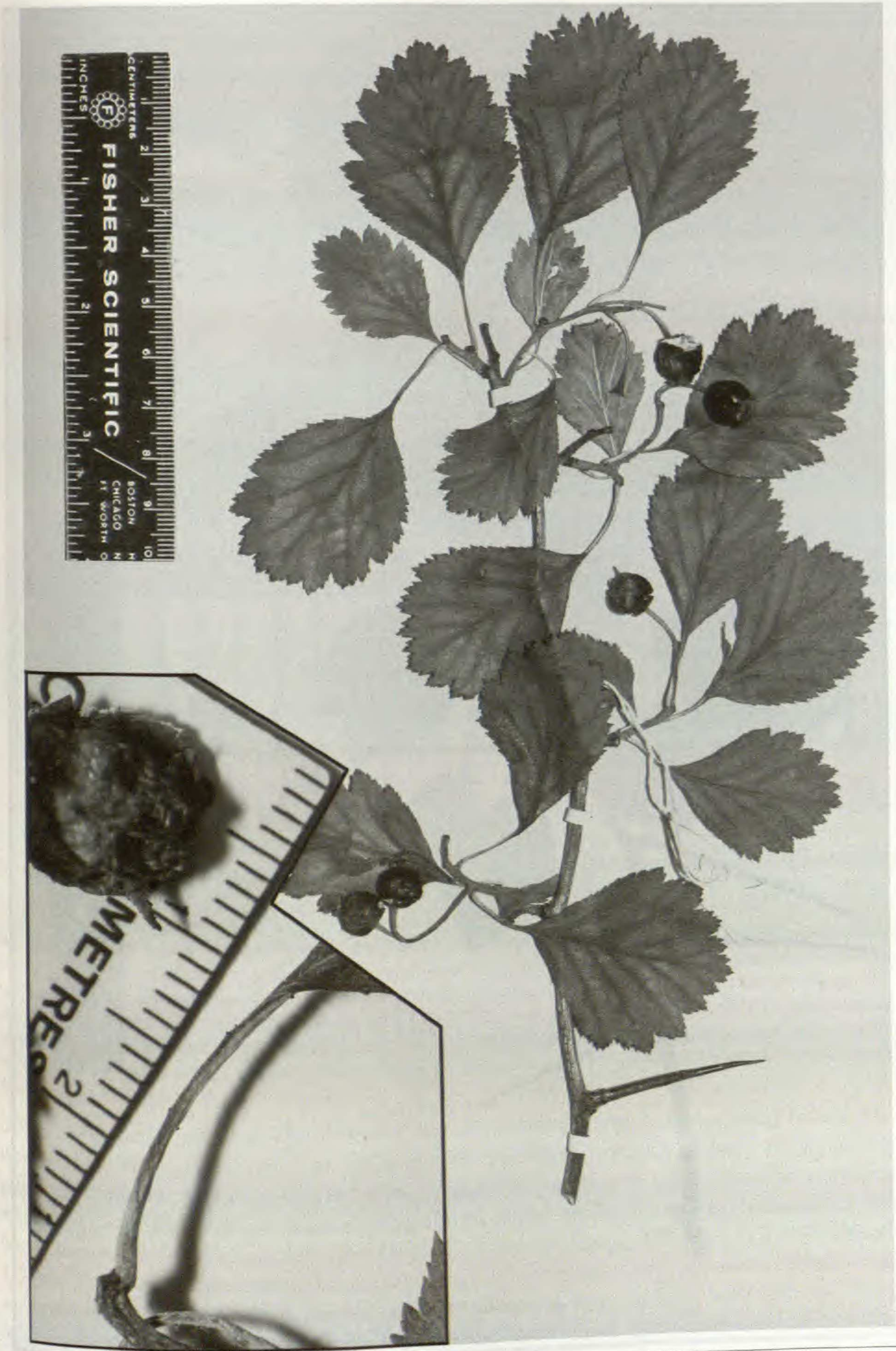


FIG. 14. Fruiting specimen of presumed *Crataegus chrysocarpa* \times *C. macracantha* (OTU 22, Phipps & O'Kennon 7103). Note leaf shape; magnification shows glands on petiole; ignore fruit on ruler. Tonasket, Washington.



FIG. 15. *Crataegus okanaganensis* var. *longispina* flowering specimen (Phipps 6962). Note large leaves, long thorns; pedicel indumentum not resolved.



FIG. 16. *Crataegus okanaganensis* var. *longispina*. Magnification of part of inflorescence (R.C. Jackson for Phipps 8416). Note dense indumentum of pedicel.

lterioribus), lobis acutis, venis 4–9(–10) per latus, marginibus serratis basi excepta, adaxialiter persistente appresso-pubescentes, abaxialiter pubescentes in venis, superficiebus pubescentibus glabrescentibus. Inflorescentiae 5–10 floratae; ramuli dense pubescentes vel subtomentosus; bracteolae caducis breve tempore, lineares, glanduloso-marginatae, glandis sessilibus sed breve-stipitatis in maioribus. Flores 12–15 mm diam.; hypanthium dense pubescens vel subtomentosum; sepala 6–7 mm longa, marginibus glandulo-denticulatis; petala late-obovata, brev-clavata; stamina 5–8, antheris albis vel pallide roseis; styli 3. Fructus urceolato-ellipsoidei, 13 mm longi, villosi, Augusti exeunte rubri, Septembri exeunte atrovinacei; reliquiae sepalorum longae, erecto-patentes vel recurvatae, marginibus glandulo-serratis; pyrenae 3, dorsale sulcatae, lateribus planis vel leviter asperibus.

Bushes, 3–8 m tall; extending twigs densely pubescent, at 1-yr. old mid- to darker, shiny reddish-brown; thorns 4–7 cm long, very dark red-brown to black, \pm slender, straight to slightly recurved. Foliage deciduous, petiolate; petioles ca. 25–30% as long as blades, \pm pubescent, densely so in sulci, eglandular or with sparse small black glands; blades rhomb-ovate (mainly) to broad-elliptic, 4.5–9(–10) cm long, often \pm convex, bases \pm broad-cuneate, (2–)3–4 lobed per side, max. LII ca. 15% (narrower leaves) –25% (broader leaves), lobes acute, 4–5 veined per side, margins serrate except near the base; adaxially persistently appressed-pubescent, abaxially surfaces scattered pubescent, glabrescent, veins pubescent. Inflorescences 5–10 flowered, branches densely pubescent to almost tomentose, bracteoles early caducous, linear, gland-margined, glands sessile except short-stipitate in larger bracteoles. Flowers 12–15 mm diam.; hypanthium densely pubescent to almost tomentose, sepals 6–7 mm long, margins glandular-denticulate; petals broad-obovate, short-clawed; stamens 5–8, anthers ivory to pale pink; styles 3. Fruit flask-shaped to ellipsoid, 13 mm long, villous, red in late August,



FIG. 17. *Crataegus okanaganensis* var. *longispina* fruiting specimen (Phipps & O'Kennon 8281). Note very large leaves; the two 4 cm thorns seen are short for this variety.

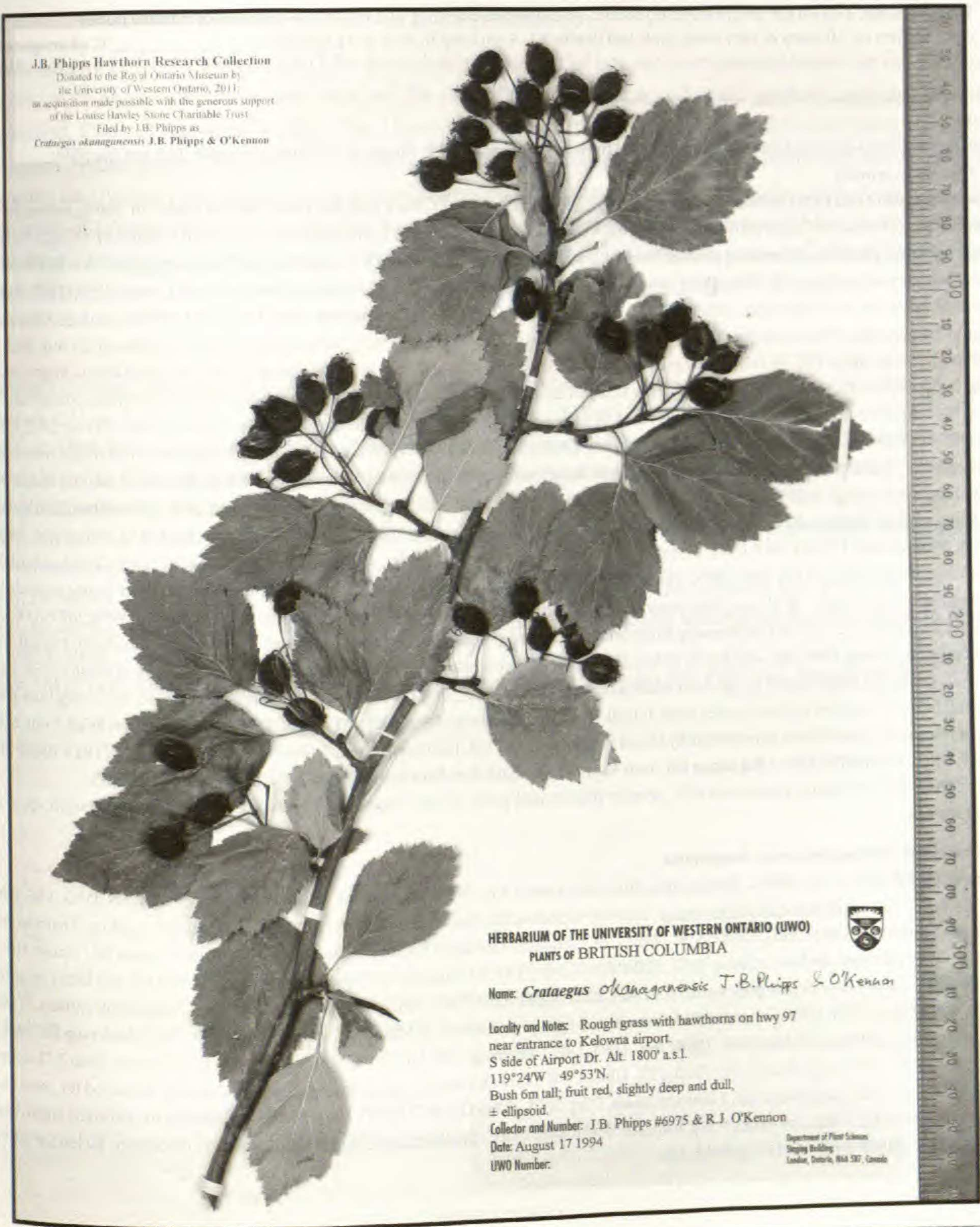


FIG. 18. *Crataegus okanaganensis* var. *okanaganensis* fruiting specimen (Phipps & O'Kennon 6975). Note much smaller leaves, shorter (ca. 2.5 cm) and proportionately stouter thorns, very sparse pedicel indumentum.

burgundy in late September, with long erecto-patent sepals or their remnants, margins glandular-serrate; nutlets 3, dorsally grooved, sides smooth to a little rough.

The key distinguishes the new variety from the other, much commoner, varieties of *Crataegus okanaganensis*.

1. Thorns ± slender, 4–7 cm long; extending shoots, inflorescence branches, and hypanthia densely pubescent; anthers 5–8, usually tinged with pink particularly when young (less commonly white*); leaf blades 4.5–9 cm long; fruit ca. 13 mm high

C. okanaganensis var. *longispina*

1. Thorns \pm stout, 2–3(–4) cm long; extending shoots, inflorescence branches, and hypanthia glabrous or \pm thinly pubescent; anthers ca. 10, ivory or very rarely pink; leaf blades 3.5–6 cm long; fruit ca. 9–12 mm high _____ **C. okanaganensis**
other varieties

*The white-anthered variant was seen at Salmon Arm.

Additional Cited Specimens [collectors abbreviated from following names: J.B. Phipps, R.J. O'Kennon, and R. Jackson (for JBP)]:

1. *Crataegus tenuior*

Flowering: BRITISH COLUMBIA: northern Okanagan, Spallumcheen Mun.: Back Enderby Road, delicate bush, 7m, young anthers strong salmon-pink, 18 May 2002, JBP 8370 (TRT, UBC); Back Enderby Road, small bush, 5 pink anthers, 23 May 2002, RJ/JBP 8400 (TRT, V); Back Enderby Road, small tree, 6 medium-pink anthers, 23 May 2002, RJ/JBP 8401 (DAO, TRT); north central Shuswap region: 2 km E of Enderby, bush 3 m, 10 pink anthers, JBP 6918, 5 May 1994 (TRT); 8 km E of Enderby, bush 4 m, 10 pink anthers, JBP 6923, 5 May 1994 (TRT); Anderson Rd., bush 5 m, 6–8 light pink anthers, RJ/JBP 8389, 22 May 2002 (TRT, UBC). **Fruiting:** BRITISH COLUMBIA: northern Okanagan, Spallumcheen Mun.: Back Enderby Road, W side, S of mailbox 5135, natural hedgerows, fruit orange-yellow to bright red, 25 Aug 2002, RJ/JBP 8451, 25.viii.2002 (TRT, WTU); Back Enderby Road, W side, S of mailbox 5135, natural hedgerows, fruit orange-yellow to bright red, 25 Aug 2002, RJ/JBP 8452 (TRT, UBC); Back Enderby Road, W side, S of mailbox 5135, natural hedgerows, fruit orange-yellow to bright red, 25 Aug 2002, RJ/JBP 8453 (TRT, V); Back Enderby Road, W side, S of mailbox 5135, natural hedgerows, fruit yellow-orange, 25 Aug 2002, RJ/JBP 8454 (DAO, TRT); Back Enderby Road, just N of Stepney Cross road, W side, S of mailbox 5135, natural hedgerows, fruit bright red-orange, 22 Sep 2002, RJ/JBP 8470 (TRT, UBC, V); Back Enderby Road, just N of Stepney Cross road, W side, S of mailbox 5135, natural hedgerows, fruit bright red-orange, RJ/JBP 8471 (DAO, TRT, UBC), Back Enderby Road, just N of Stepney Cross road, W side, S of mailbox 5135, natural hedgerows, fruit bright red-orange, RJ/JBP 8472 (TRT, V); north central Shuswap region: 2 km E of Enderby, bush 3 m, fruit scarlet, 25 Sep 1993, JBP & O'K 6811 (DAO, TRT, UBC, V); 5 mi E of Enderby, bush 3 m, fruit scarlet, 25 Sep 1993, JBP & O'K 6814 (TRT); 5 mi E of Enderby, bush 3 m, fruit scarlet, 25 Sep 1993, JBP & O'K 6814a (CAN, DAO, TRT, UBC, V, WTU); Ca. 200 m E of Shuswap River bridge on Enderby-Mabel Lake Road, S side, top of river bank among scrub, slender bush, 4 m tall, fruit light salmon, type bush, 20 Aug 1994, JBP & O'K 7011 (TRT, UBC, WTU); ca. 200 m E of Shuswap River bridge on Enderby-Mabel Lake Road, S side, edge of swampy woods, bush, 3 m tall, fruit light salmon, 20 Aug 1994, JBP 7013 & O'K (DAO, TRT); Valley of the Shuswap, ca. 8 km E of Enderby, a little to the E of Brash Creek, S side of road, woodland edge, bush 4 m tall, fruit salmon-orange, 20 Aug 1995, JBP 7171 (TRT, V), Anderson Road, S side, at 1.5 telephone posts beyond farm surrounded by lots of pines, bush 3m tall, fruit reddish-orange, 7 Sep 2001, JBP & O'K 8274 (TRT); Anderson Road, S side, at 1.5 telephone posts beyond farm surrounded by lots of pines, bush 6 m tall, fruit orange-red, 7 Sep 2001, JBP & O'K 8275 (TRT); RJ/JBP 8474 (TRT, UBC). **WASHINGTON: Okanogan Co.**: near Palmer Lake, bush 3 m, fruit scarlet, 4 Sep 2001, JBP & O'K 8265 (TRT).

Note that duplicate specimens of *C. tenuior* distributed prior to this paper were probably identified as *Crataegus* sp. or *C. macracantha*.

2. *Crataegus okanaganensis* var. *longispina*

Flowering: BRITISH COLUMBIA: Salmon Arm, dump site, bush 2.5 m, 5–6 white anthers, 10 May 1994, JBP 6962 (CAN, DAO, TRT, UBC, UVIC, V, WTU); north central Shuswap region: Enderby-Grindrod Rd., between Anderson Rd. and Inch Logan Rd., sapling, 5 ivory to very pale pink anthers, 22 May 2002, RJ/JBP 8392 (TRT, UBC); Enderby-Grindrod Rd., betw. Anderson Rd. and Inch Logan Rd., (small) tree, 5 ivory to very pale pink anthers, 22 May 2002, RJ/JBP 8393 (CAN, TRT, V); Enderby-Grindrod Rd., betw. Anderson Rd. and Inch Logan Rd., mature tree, 5 ivory to very pale pink anthers, 22 May 2002, RJ/JBP 8394 (TRT, UBC); Anderson Rd., bush 8 m, 5 light pink anthers, 31 May 2002, RJ/JBP 8415 (TRT, UBC); Anderson Rd., bush 8 m, 5 light pink anthers, 31 May 2002, RJ/JBP 8416 (DAO, TRT); Anderson Rd., bush 8 m, anthers old, darkened, 31 May 2002, RJ/JBP 8417 (TRT, UBC). **Fruiting:** BRITISH COLUMBIA: Salmon Arm, dump site, bush 2.75 m, fruit red, 20 Jul 1994, JBP & O'K 7026 (CAN, DAO, TRT, UBC, UVIC, V, WTU); north central Shuswap region: Enderby-Grindrod Rd., near Inch Logan Rd., 3 m bush, burgundy fruit, 5 filament bases, 7 Sep 2001, JBP & O'K 8273 (TRT); Hwy. 97A, N of Enderby, nr. Jim's fruit stand, bush 3 m, fruit plum-red, 5 filament bases, 7 Sep 2001, JBP & O'K 8282 (TRT). Spallumcheen Mun.: W side Rd., NW of Vernon, 3.5 km S of jct. 97, 25 Aug 2002, RJ/JBP 8463 (TRT) is possibly this.

CONCLUSIONS

Although earlier treatments of the *Crataegus* flora of British Columbia and adjacent Washington (e.g., Hitchcock & Cronquist 1973; Taylor 1973; Brayshaw 1996) reported few species for the area, intensive collecting between 1993 and 2002 in the greater Okanagan has yielded a further eight species and several varieties of this genus (Phipps & O'Kennon 1998, 2002, 2004). Thus, far from a position that the northern Okanagan-south-eastern Shuswap is of no special evolutionary interest, perhaps true for many groups of plants, it is clear that the area is a Nirvana for hawthorns: it is mesic, it has sufficient open habitat and the temperature band is favorable.

This paper supersedes the relevant parts of the author's treatment for *Crataegus* in *Flora of North America*, volume 9.

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I wish to thank Bob O'Kennon of BRIT for many happy and fruitful hours of companionship in the field during the discovery process for these new taxa and for several photographs as indicated on their captions. Antony Littlewood, Dept. of Classical Studies, The University of Western Ontario, is thanked for checking the Latin diagnoses. Nadia Talent, University of Toronto, and Tim Dickinson, University of Toronto and Royal Ontario Museum, are thanked for comments on an earlier version of the manuscript. Alan Noon, Dept. of Biology, The University of Western Ontario, is thanked for photography of herbarium specimens and Ian Craig, Imaging Unit, Dept. of Biology, The University of Western Ontario, for his assistance in preparing the figures for the paper. Financial assistance for publication was provided by Barney Lipscomb and Bob O'Kennon.

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